PHYSIOLOGY OF THE WHITE CHROMATOPHORES IN THE FIDDLER CRAB, UCA PUGILATOR [1]

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A survey of the literature on chromatophores (Fingerman, 1965) reveals that much more information is available concerning the control of melanophores in the fiddler crab, *Uca pugilator,* than about its white chromatophores. Brown and Sandeen (1948) reported that the white chromatophoric pigment of *Uca pugilator* from the region of Woods Hole, Massachusetts, was more dispersed in animals on a white background than on a black background. The white pigment as well as the melanin of *Uca pugilator* also exhibited a daily rhythm whereby both pigments were more dispersed during the daytime than at night (Brown and Webb, 1948).

Removal of both eyestalks from *Uca pugilator* results in concentration of the melanin (Carlson, 1935) ; extracts of the sinus glands cause its dispersion (Sandeen, 1950). The white chromatophores respond differently to eyestalk removal; the white pigment becomes maximally dispersed. Furthermore, subsequent injection of extracts of sinus glands did not alter this state in Woods Hole crabs. However, Sandeen did find a high concentration of white pigment-concentrating hormone in the circumesophageal connectives. Because the white chromatophoric pigment of the assay animals used by Sandeen was initially maximally dispersed she could demonstrate only a white pigment-concentrating hormone. She also postulated that an antagonism exists between the melanin-dispersing hormone and the white pigment-concentrating hormone, such that the presence of a large amount of the former decreases the expression of the latter. At that time no evidence was available for the presence of a white pigment-dispersing substance in any crab. Recent studies on *Rhithropanopeus harrisi* (Pautsch *et al.,* 1960), *Carcinus maenas* (Powell, 1962a), *Ocypode platytarsis* (Nagabhushanam and Rao, 1964), *Ocypode macrocera* (Rao, 1967), and *Uca annulipes* (Nagabhushanam and Rao, 1967) have, however, revealed that the white chromatophores in each of these crabs are controlled by two hormones, pigment-concentrating and pigment-dispersing. Therefore, it was decided to reinvestigate the endocrine control of the white chromatophores of *Uca pugilator* to determine whether evidence for a white pigment-dispersing substance could be obtained with this crab also.

To assay for white pigment-dispersing and -concentrating substances it was necessary to obtain two sets of assay animals, one with white pigment in a concentrated state and the other in a maximally dispersed state. In a preliminary experiment it was found that fiddler crabs obtained from Panacea, Florida, would be suitable assay animals. The responses of the white chromatophores of these crabs to light and background were quite different from those reported for Woods Hole

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crabs by Brown and Sandeen (1948). The experiments described below deal with the (a) daily rhythm of pigment migration in the white chromatophores, (b) responses of the white chromatophores to light and background, (c) endocrine control of the white chromatophores, and (d) antagonism among the substances controlling the black and the white chromatophores of *Uca pugilator* from Panacea, Florida.

Materials and Methods

The animals used in this investigation were specimens of *Uca pugilator* collected in Panacea, Florida, and shipped to New Orleans. In the laboratory the crabs were maintained in stainless steel tanks containing a small amount of artificial sea water. Crabs of 14–17 mm. carapace width were used without regard to sex. At least one day before the crabs were used in an experiment the large chela of the males was removed for convenience in handling them. Eyestalkless crabs which were utilized as assay animals had had their eyestalks ablated at least 12 hours before use.

Extracts of sinus glands, optic ganglia, supraesophageal ganglia, circumesophageal connectives, and thoracic ganglia were prepared in crustacean physiological saline (Pantin, 1934) in the manner described by Sandeen (1950). In addition to preparation of saline extracts, these tissues were extracted with acetone in order to obtain acetone-soluble and acetone-insoluble fractions. The tissue to be fractionated was freshly dissected from the crabs and placed in an embryological watch glass. After preliminary drying at room temperature for 10 minutes the tissue was triturated with a glass rod and extracted with acetone, 1 ml. per organ. The extract was centrifuged for 10 minutes at 1500 *g* and the liquid was decanted into a porcelain evaporating dish and allowed to evaporate. The residue was then extracted in saline to obtain the acetone-soluble fraction. The acetone was free of water when it was first poured on the tissue. The insoluble material was then allowed to dry and extracted with saline, providing the acetone-insoluble fraction.

The dose of each extract injected into an assay animal was 0.05 ml. The extracts were prepared in the following concentrations per dose: one sinus gland, the optic ganglia from one eyestalk, the supraesophageal ganglia from one crab, one circumesophageal connective, and one-half the thoracic ganglia from a single crab.

Each extract was injected into 10 eyestalkless crabs whose white pigment was maximally dispersed and into 10 crabs whose white pigment was maximally concentrated as a result of adaptation for two hours on a black background. The controls, which consisted of eyestalkless crabs and crabs adapted to a black background, received injections of saline in a dose of 0.05 ml./crab. Each experiment was repeated once. All the experiments were conducted during the daytime.

The chromatophores on the walking legs were staged according to the scheme of Hogben and Slome (1931). Stage 1 represents maximal pigment concentration, stage 5 maximal dispersion, and stages 2, 3, and 4 the intermediate conditions.

In order to facilitate comparison of the responses to the several extracts activity values were calculated in the manner described by Sandeen (1950). In each experiment the average stage of the white pigment was recorded at the start of the experiment and 15 and 30 minutes after the extracts had been injected and at 30-minute intervals thereafter for the duration of the response. When pigment

dispersion occurs the sum of the average chromatophore stages recorded throughout the experiment for the control group is subtracted from the sum for the experimental group. When pigment concentration occurs the sum for the experimental group is subtracted from the sum of the control group. The differences represent the activity values and constitute a measure of both the intensity and duration of the response.

Experiments and Results

Rhythm of white pigment migration

This experiment was conducted using a group of crabs delivered to the laboratory on March 21, 1967. On that afternoon 40 intact crabs were placed in a plastic container with a small volume of sea water, about 0.5 cm. deep. The container was covered with two layers of black cloth to provide darkness for the crabs. Another lot of 40 was selected and distributed 10 each into two white and two black enameled basins which were kept under a constant illumination of 3.25 meter-candles light intensity. At noon on March 22 the average stage of the white chromatophores of 20 crabs adapted to darkness was determined and the crabs were returned to darkness. The white chromatophores of the crabs on black and white backgrounds were also staged and the crabs returned to their respective backgrounds. This procedure was repeated every four hours through midnight of March 25 and the results are shown in Figure 1. The white pigment of the crabs maintained in constant darkness was more dispersed during the daytime than at night. However, there was no evidence of rhythmical migration of the white pigment of the crabs kept under constant illumination on either background. The white pigment of the crabs on the black background was maximally concentrated while on a white back-

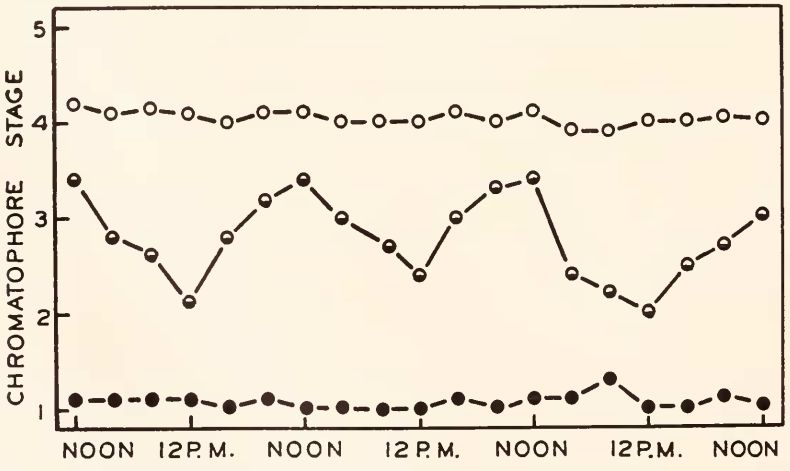

Figure 1. Relationships between the stage of the white chromatophores and time of day for crabs maintained in darkness (half-filled circles), in constant light (3.25 meter-candles) on a white background (circles), and in constant light (3.25 meter-candles) on a black background (dots). Observations began at noon of March 22, 1967.

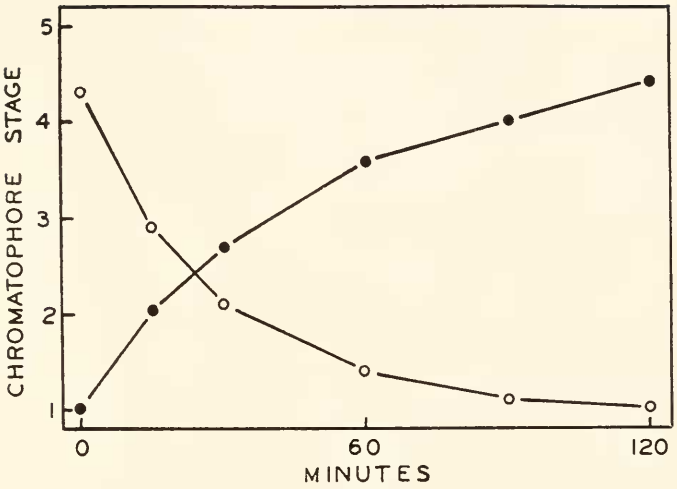

FIGURE 2. Responses of the white chromatophores of *Uca pugilator* to a change of background. Crabs changed from a black background to white (dots), from a white background to black (circles).

ground the pigment was almost maximally dispersed. These results show that in *Uca pugilator* from Panacea, Florida, the background response overrides the daily rhythm at this intensity of incident illumination.

Time required to achieve maximal chromatic adaptation

Twenty specimens of *Uca pugilator* were taken from the stock aquaria and divided into two groups of 10 crabs each. One group was placed in a white enameled basin and the second group in a black enameled basin. At 9 AM both containers were placed under an illumination of 3.25 meter-candles light intensity. At 11 AM the average stage of the white chromatophores in the crabs from each pan was determined. The crabs that had been on a white background were then placed on a black background and *vice versa*. The chromatophore stages of the crabs in each basin were subsequently determined 15, 30, 60, 90 and 120 minutes after the backgrounds had been interchanged. This experiment was repeated once and the averaged data were used in the preparation of Figure 2. As is evident from the figure, the white pigment of crabs on a black background became maximally concentrated. On a white background the white pigment was nearly maximally dispersed. Background adaptation was complete in two hours. The chromatophore stages of the crabs adapted to these backgrounds are essentially the same as seen in Figure 1 for the crabs on the same backgrounds.

Relationships between chromatophore stage and incident light intensity

Ten crabs were placed into each of seven black and seven white basins at 8:30 AM. The crabs in one black and one white container were then exposed

for two hours to one of the following intensities of light: 0.19, 0.93, 4.65, 26.0, 52.1, 103.1, and 408.0 meter-candles. Then the white chromatophores of each crab in the 14 basins were staged. This experiment was repeated once. The means of the data obtained from these experiments were used in the preparation of Figure 3. The white pigment of the crabs in black pans remained maximally concentrated at light intensities up to 52.1 meter-candles, but at the higher intensities the pigment dispersed somewhat.

The white pigment of the crabs in the white pan at 0.19 meter-candle light intensity was only dispersed to an intermediate state. As the light intensity increased the degree of dispersion increased to the maximum, stage 5, at 26.0 meter-candles and remained so at all the higher intensities tested.

The next experiment was aimed to determine the relationship between the degree of white pigment dispersion in the chromatophores of eyestalkless Panacea *Uca pugilator* and the intensity of incident illumination. In eyestalkless *Uca pugilator* from Woods Hole the white pigment was in a maximally dispersed state (Sandeen, 1950). In contrast, the white pigment of the Panacea crabs did not respond consistently to eyestalk ablation. Among eyestalkless individuals exposed to a light intensity of 3.25 meter-candles 47% had their white pigment in stage 5, 9% in stage 4, 17% in stage 3, 4% in stage 2, and 23% in stage 1. From a group of eyestalkless crabs 35 individuals with their white pigment in stage 5 and 35 with their white pigment in stage 1 were selected and distributed five each among 14 white enameled basins. One container holding crabs with maximally dispersed white pigment and another with crabs having maximally concentrated white pigment were exposed to one of the light intensities used in the preceding experiment for two hours. Then the chromatophores of each crab in the 14 basins were staged. This experiment was performed three times. The mean chromatophore stages

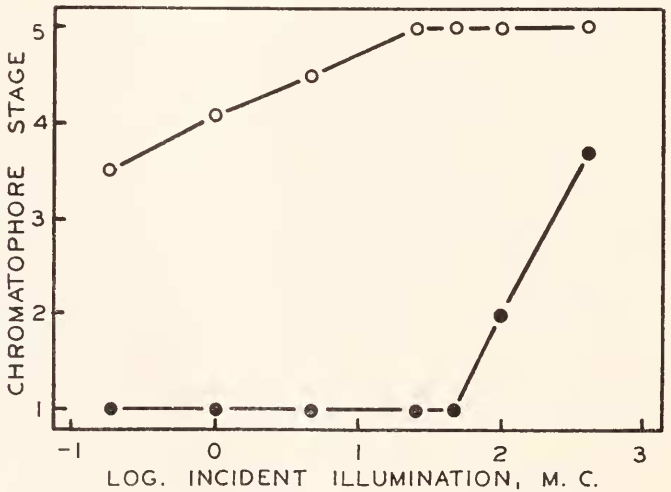

FIGURE 3. Relationships between the stage of the white chromatophores and the logarithm of the incident light intensity in meter-candles for intact crabs during the daytime on a black background (dots) and on a white background (circles).

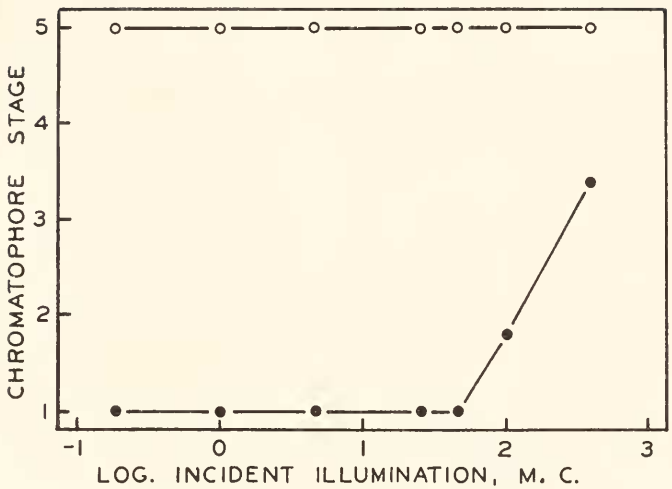

FIGURE 4. Relationships between the stage of the white chromatophores of eyestalkless *Uca pugilator* and the logarithm of the incident light intensity in meter-candles. One group was chosen because its white pigment was maximally concentrated at the low light intensities (dots) while in the other (circles) it was maximally dispersed.

were used in the preparation of Figure 4 where each point represents the average stage of 15 crabs. The degree of pigment dispersion in the chromatophores of the eyestalkless crabs with maximally dispersed white pigment did not change with alteration of the incident light intensity. The concentrated white pigment was also unaffected by light intensities up to 52.1 meter-candles. But at light intensities above 52.1 meter-candles the pigment showed some dispersion with increasing light intensity just as in the intact crabs (Fig. 3) where high light intensities fostered pigment dispersion. This effect is a primary response to light.

Substances controlling the white chromatophores

The aim of this set of experiments was to determine whether or not a pigment-dispersing as well as a pigment-concentrating substance was involved in the control of pigment migration in the white chromatophores of *Uca pugilator*. The activity values for saline extracts of the sinus glands, optic ganglia, supraesophageal ganglia, circumesophageal connectives, and thoracic ganglia injected into eyestalkless *Uca pugilator* and into intact specimens with maximally concentrated white pigment as a result of having kept intact crabs on a black background are shown in Table I. Neither physiological saline nor muscle extracts had any effect whatever on the white pigment whether it was originally concentrated or dispersed.

The saline extracts of the sinus glands, optic ganglia, supraesophageal ganglia, and thoracic ganglia had no effect on the initially dispersed white pigment but did cause dispersion of this pigment. In contrast, the circumesophageal connectives had a pronounced white pigment-concentrating effect but evoked no white pigment-dispersing response.

TABLE I

Activity values for extracts of the sinus glands, central nervous organs, and muscle

	Aqueous extract		Acetone-soluble fraction		Acetone-insoluble fraction	
	Dispersion	Concentration	Dispersion	Concentration	Dispersion	Concentration
Sinus gland	20.0	0.0	0.0	3.4	21.6	0.0
Optic ganglia	18.6	0.0	0.0	7.0	23.4	0.0
Supraesophageal ganglia	13.2	0.0	0.0	0.8	16.8	0.0
Circumesophageal connectives	0.0	12.3	0.0	11.9	0.0	0.0
Thoracic ganglia	13.8	0.0	0.0	6.0	16.0	0.0
Muscle	0.0	0.0	0.0	0.0	0.0	0.0

The acetone-soluble fraction of the sinus glands and central nervous organs evoked in every case at least some white pigment concentration but in no case caused dispersion of the white pigment (Table I). The acetone-insoluble material of the sinus glands, optic ganglia, supraesophageal ganglia, and thoracic ganglia caused no concentration of the white pigment but did cause dispersion of this pigment (Table I). The acetone-insoluble material of the circumesophageal connectives contained neither the white pigment-concentrating nor white pigment-dispersing hormone.

Antagonism between the white pigment-concentrating substance and the white pigment-dispersing substance

The following experiment was devised in consideration of the antagonism that Sandeen (1950) reported between the white pigment-concentrating and melanin-dispersing hormones. Extracts of the supraesophageal ganglia and the circumesophageal connectives from 20 crabs were prepared, each in 1 ml. of physiological saline. One-half ml. of each of these extracts was then diluted with an equal volume of physiological saline. Equal volumes of the two original extracts were then combined to produce a single extract consisting of one-half a complement of the supraesophageal ganglia and circumesophageal connectives per 0.05 ml. Each of the three resulting extracts was injected into 10 eyestalkless crabs and 10 intact crabs with maximally concentrated white pigment. With the eyestalkless crabs melanin-dispersing and white pigment-concentrating activities were determined while with the intact crabs the white pigment-dispersing activity was determined. This experiment was repeated once and the averaged results are shown in Figure 5.

The extracts of the supraesophageal ganglia alone dispersed both the melanin of the eyestalkless crabs (Fig. 5A) and the white pigment of the intact crab on the black background (Fig. 5B) but, as in Table I, did not concentrate the white pigment. The extracts of the circumesophageal connective alone dispersed the melanin and concentrated the white pigment of eyestalkless crabs (Fig. 5C) but, as in Table I, had no effect on the white chromatophores of crabs on a black background (Fig. 5D). The mixture of the supraesophageal ganglia and circumesophageal connectives dispersed the melanin and concentrated the white pigment of eyestalkless crabs

(Fig. 5E) and dispersed the white pigment of intact crabs on a black background (Fig. 5F). The activity values for the three extracts in decreasing order of melanin-dispersing potency are for the supraesophageal ganglia plus the circumesophageal connectives (20.3), supraesophageal ganglia alone (19.2), and circumesophageal connectives alone (9.6). A similar listing for white pigment-dispersing activity is for the supraesophageal ganglia alone (11.2), supraesophageal ganglia plus the circumesophageal connectives (5.8), and circumesophageal connectives alone (0.0). For white pigment-concentrating activity the sequence is circumesophageal connectives alone (11.9), supraesophageal ganglia plus the circumesophageal connectives (2.5), and supraesophageal ganglia alone (0.0). These results demonstrate that when the extracts of circumesophageal connectives and supraesopageal ganglia are mixed the hormones that concentrate and disperse the white pigment are inhibited considerably. The fact that the extract of the circumesophageal connectives produced a melanin-dispersing activity of 9.6 but no dispersion of the white pigment

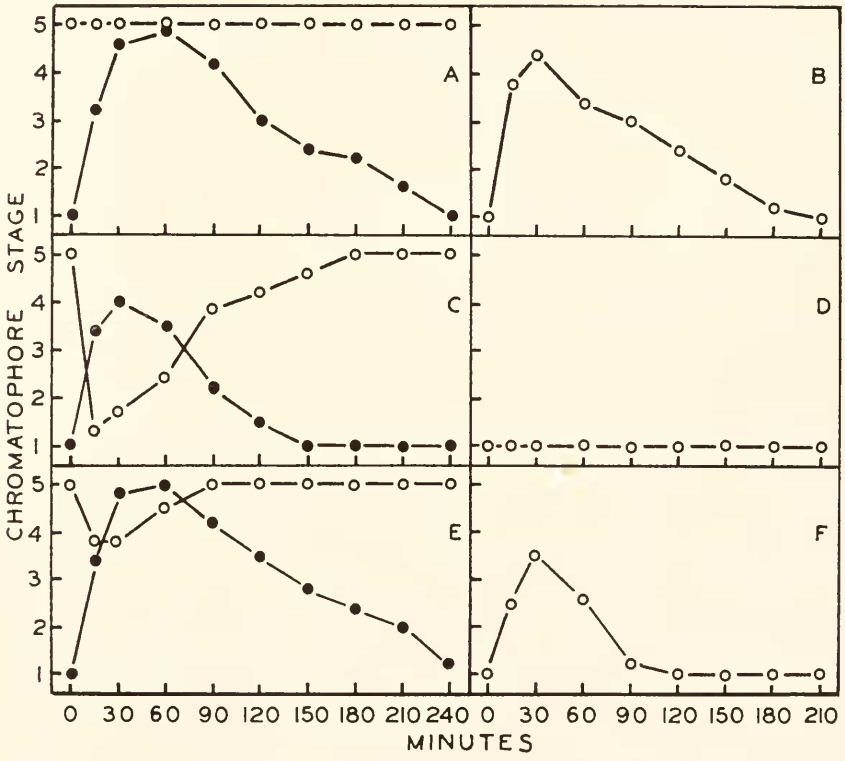

FIGURE 5. Relationships between the stage of the melanophores (dots) and white chromatophores (circles) and time following injection of extracts prepared in physiological saline of the supraesophageal ganglia (A and B), circumesophageal connectives (C and D), and a mixture of equal volumes of these extracts of the supraesophageal ganglia and circumesophageal connectives (E and F) into eyestalkless crabs (A, C, and E) and intact crabs adapted to a black background (B, D, and F). See text for complete explanation.

makes it highly unlikely that dispersion of these two pigments could be due to one hormone. These data will be discussed further below.

Discussion

When the Panacea *Uca pugilator* were maintained in constant darkness the white chromatophoric pigment exhibited a daily rhythm of pigment migration (Fig. 1); the pigment was more dispersed during the daytime than the night. A similar rhythm has been reported for the white chromatophores of *Uca pugilator* from Woods Hole (Brown and Webb, 1948) and *Uca annulipes* (Rao and Nagabhushanam, 1967). However, the amplitude of the rhythm observed for the white pigment of *U. pugilator* from Panacea, Florida, and *U. annulipes* kept in darkness was less than that reported for *U. pugilator* from Woods Hole. The white chromatophoric pigment of *Carcinus maenas* (Powell, 1962b) and *Rhithropanopeus harrisi* (Pautsch *et al.,* 1960) maintained in darkness showed no rhythmicity.

The *Uca pugilator* from Panacea exhibited a pronounced background adaptation. The degree of background adaptation achieved by these individuals was uninfluenced by rhythmicity of the chromatophoric pigment observed in the crabs kept in darkness. In contrast, in Woods Hole *Uca pugilator* the rhythm is a very strong factor in determining the degree of pigment dispersion in the chromatophores of crabs on black and on white backgrounds (Brown and Sandeen, 1948).

The responses to increased illumination of the white chromatophores of *Uca pugilator* from Panacea and Woods Hole were qualitatively alike. In both intact and eyestalkless specimens greater dispersion of the white pigment occurred as the total illumination increased. In contrast, the white pigment of *Uca annulipes* (Rao and Nagabhushanam, 1967) failed to exhibit a true background response; the degree of pigment dispersion was dependent only on the intensity of reflected light.

Of all the extracts prepared in physiological saline only those of the circumesophageal connectives failed to disperse the white pigment in the *Uca pugilator* from Panacea. Sandeen (1950) was unable to determine the existence of the white pigment-dispersing hormone in the *Uca pugilator* from Woods Hole because she used crabs with maximally dispersed white pigment only. Herein evidence is provided for the first time for the presence of a white pigment-dispersing substance in *Uca pugilator.* Although the extracts of the optic ganglia, sinus glands, supraesophageal ganglia, and thoracic ganglia that were prepared in physiological saline provoked white pigment dispersion in *Uca pugilator,* they had no effect on initially dispersed white pigment. However, by using acetone fractionation it was possible to demonstrate the presence of both white pigment-concentrating and -dispersing hormones in all of the organs tested except the circumesophageal connectives. The acetone-soluble fraction of all the tissues had the white pigment-concentrating hormone while the acetone-insoluble fraction of all but the circumesophageal connectives had the white pigment-dispersing hormone. The white pigment-dispersing hormone of *Ocypode* also is insoluble in acetone while the white pigment-concentrating hormone is soluble in this solvent (Nagabhushanam and Rao, 1964; Rao, 1967).

Among the crabs that have been investigated so far the distribution in the nervous system of *Uca pugilator* of the two substances affecting white pigment is

unique. The circumesophageal connectives of *Uca pugilator* possess only one of the two substances, the white pigment-concentrating hormone, while the optic ganglia, sinus glands, supraesophageal ganglia, and thoracic ganglia contain both. In contrast, the circumesophageal connectives of *Ocypode platytarsis* (Nagabhushanam and Rao, 1964), *Ocypode macrocera* (Rao, 1967), *Uca annulipes* (Nagabhushanam and Rao, 1967) and *Carcinus maenas* (Powell, 1962a) possess both. In both species of *Ocypode* and *Uca annulipes* the optic ganglia, sinus glands, supraesophageal ganglia, and thoracic ganglia also contain both. In *Rhithropanopeus harrisi,* however, the white pigment-dispersing hormone was found only in the eyestalk (Pautsch *et al.,* 1960), and Powell (1962a) noted that the white pigment-dispersing and -concentrating hormones of *Carcinus maenas* were restricted to the thoracic ganglia and circumesophageal connectives.

As mentioned above, Sandeen (1950) concluded from her experiments that a large quantity of melanin-dispersing hormone decreased the expression of the white pigment-concentrating hormone. When an extract of the circumesophageal connectives was mixed with the extract of supraesophageal ganglia (Fig. 5) the white pigment-dispersing activity of the latter was reduced while the melanin-dispersing activity increased slightly because both tissues contained the melanin-dispersing hormone. In view of the presence in *Uca pugilator* of a white pigment-dispersing hormone, as well as the white pigment-concentrating hormone, a more likely explanation of the antagonism that Sandeen observed is that the antagonism was between the white pigment-dispersing substance and the white pigment-concentrating hormone and that it was merely a coincidence that the extracts she used contained both the melanin-dispersing and white pigment-concentrating hormones.

Although it was shown by the acetone fractionation that the optic ganglia, sinus glands, thoracic ganglia, and supraesophageal ganglia of *Uca pugilator* contain both the white pigment-dispersing and -concentrating hormones, the extracts prepared in physiological saline caused white pigment dispersion only. We could not demonstrate the white pigment-concentrating hormone in the extracts that were prepared directly in physiological saline. If this hormone is present in the saline extracts, then the white pigment-dispersing substance completely inhibited the expression of the white pigment-concentrating hormone. Another possibility is that the latter hormone may be present in the tissues in an inactive (precursor) state, and as such may not be soluble in water. Acetone could act on the precursor liberating an active hormone which is soluble in both acetone and water. If the second possibility is the correct one, then the state in which the white pigment-concentrating hormone occurs in the circumesophageal connectives would have to be different from that in the other parts of the nervous system. It will be recalled that the white pigment-concentrating hormone of the circumesophageal connectives is readily soluble in water (Table I). Moreover, after acetone fractionation of the circumesophageal connectives no increase in white pigment-concentrating activity was observed. In contrast, the presence of white pigment-concentrating hormone in the other tissues was demonstrable only after they were extracted in acetone.

The question was raised above concerning the possibility that the melanin-dispersing hormone and white pigment-dispersing hormone are the same substance and it was concluded from the data of Figure 5 that it is highly unlikely. The fact

that the melanin is maximally concentrated in eyestalkless individuals but their white pigment, as mentioned above, was found in all possible stages from maximally concentrated to maximally dispersed also would not be consistent with a unihormonal hypothesis. An intact crab can on occasion even show maximal dispersion of its melanin while its white pigment is maximally concentrated.

The difference between the relative importance of the background response and biological clock in determining the stage of the white pigment of the Panacea and Woods Hole *Uca pugilator* is the second observed difference among these populations with respect to their pigmentary systems. A daily rhythm of melanin migration in both intact and eyestalkless *Uca pugilator* from Florida, has been observed (Fingerman and Yamamoto, 1967), but so far not in Woods Hole fiddler crabs whose eyestalks had merely been removed (Fingerman, Couch and Stool, 1966). Fingerman (1966) has, however, been able to restore the rhythm in eyestalkless fiddler crabs from Woods Hole by implanting sinus glands. Further comparative investigation may reveal more differences between the fiddler crabs of these two populations.

Summary and Conclusions

1. Specimens of the fiddler crab, *Uca pugilator,* from Panacea, Florida, exhibited a daily rhythm of migration of their white chromatophoric pigment only when maintained in constant darkness. The pigment was more dispersed by day than at night. Crabs exposed to an incident illumination of 3.25 meter-candles on black and on white backgrounds showed no rhythm.

2. The white pigment of these fiddler crabs exhibited a strong background adaptation. The pigment was well dispersed in crabs on a white background and maximally concentrated in those on a black background.

3. At an incident light intensity of 3.25 meter-candles the white pigment of only 47% of the eyestalkless crabs was maximally dispersed. In 23% of the eyestalkless crabs it was in a maximally concentrated state. High intensities of illumination induced dispersion of the white pigment.

4. Evidence was presented for the first time for the presence of a white pigment-dispersing substance in the sinus glands and central nervous system of *Uca pugilator.* The optic ganglia, sinus glands, supraesophageal ganglia, and thoracic ganglia contain white pigment-dispersing and -concentrating substances. Extracts of these tissues prepared directly in physiological saline revealed only the white pigment-dispersing hormone. However, fractions obtained by acetone extraction of these tissues evoked white pigment concentration while the acetone-insoluble material evoked white pigment dispersion.

5. The circumesophageal connectives are, in contrast, devoid of the white pigment-dispersing substance. They do, however, evoke melanin dispersion in eyestalkless *Uca.*

6. The white pigment-concentrating and -dispersing substances appear to be mutually antagonistic.

7. The question of the possible identity of the melanin-dispersing and white pigment-dispersing substances was discussed. The data suggest that this is a highly unlikely possibility.

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